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THE STATUS OF THE ALGO-LICHEN HYPOTHESIS.

BY THOMAS A. WILLIAMS.

IN treating this subject it will not be out of place to give first a short history of the growth of knowledge concerning lichens and their structure. The earlier lichenologists knew but very little of lichens as now understood, and comparatively nothing as to their internal structures. As the magnifying power of microscopes was increased, so the knowledge of the lichen thallus was increased. The affinities of lichens to the discomycetous fungi on the one hand and to the algæ on the other were early noticed and commented upon, and some species have been alternately placed among the fungi, then among the lichens, and others have been repeatedly changed from lichens to algæ, and vice versa. Later authors, as Cornu and Tulasne, consider the lichen very near if not belonging to the Ascomycetes, while De Bary, Krabbe, and others place them among the Ascomycetes without any doubt as to that being the proper place for them.¹ Lately *Cora* and several other genera have been placed among the lichens under the name of *Hymenolichens*—*i.e.*, lich-

¹ Stahl found the reproductory organs of *Collema* to be very similar to those of the Discomycetes. Borzi confirmed Stahl's observations by his own. Fünfstück, after a study of the development of the apothecia of *Peltigera* and *Nephroma*, believed that "the reproduction is by apogamy, with rudimentary sexual organs, as in *Podosphæra* among the Discomycetes." De Bary says (*Morph. and Biol. of Fungi*, etc.): "The formation of the perithecia of lichens from the primordial coils of hyphæ follows in general the same course as that of *Xylaria*, *Polystigma*, etc." This is confirmed by the observations of Krabbe, Füsting, and others who have made an extended study of the *Cladoniæ*, *Sphyridium*, *Lecanora*, *Lecidea*, etc.

ens which, according to Johow, are made up of the hyphal elements of a hymenomyceteous fungus and an alga. Masee claims to have discovered a Gasterolichen. So that now we have lichens placed among the Ascomycetes and the Basidiomycetes, and by good authority.

Wallroth (1825) was the first to make any study of the gonidia. He was followed by Koerber (1839), who studied them more fully than did Wallroth. But not until 1851 was made anything like an explanation as to their probable origin and subsequent growth. This was done by Bayrhoffer. He asserted that the gonidia came from the "fibrous stratum, the fibres of which swelled at the top and produce male gonidia." Speerschnieder, who was the next to study the gonidia, differed from Bayrhoffer on some points, but agreed as to their probable origin. Schwendener, in his earlier works, took a similar view, basing his argument on the fact that the gonidia, many of them, seemed to be connected with the ends of the hyphæ. De Bary, in his work of 1865, agreed with Schwendener as to the heteromerous lichens, but in case of such species as belong to the Collemaceæ, etc., he said: "Either the lichens in question are the perfectly developed states of plants whose imperfectly developed forms have hitherto stood among the algæ as Nostocaceæ and Chroococceæ, or the Nostocaceæ and Chroococceæ are typical algæ, which assume the form of *Collema*, *Ephebe*, etc., through certain parasitic Ascomycetes penetrating into them, spreading their mycelium into the continuously growing thallus and becoming attached to their phycochrome-containing cells." This gave to Schwendener the idea of *dualism* which he afterward formulated and presented to the world. Such was the beginning of the much-debated "Algo-Lichen hypothesis." Schwendener in this famous theory declares that all lichens, so-called, are dual organisms, consisting of a fungus, parasitic upon an alga, whole colonies of which it envelops with hyphæ. These algæ he divides into two classes, Phycochromaceæ, or those with bluish-green coloring matter, phycochrome, and Chlorophyllaceæ, or those containing chlorophyll. The first of these he divides into five types: 1, Sirospioneæ; 2, Rivulariæ; 3, Scytone-mæ; 4, Nostocaceæ; 5, Chroococceæ. The latter he separates into three types: 1, Confervaceæ; 2, Chroolepideæ; 3, Palmellaceæ. To some one of these types, he claimed, the gonidia of every lichen could be referred.

About this time Famentzin and Baranetzky by cultivating the gonidia of several lichens (*Physcia* [*Theloschistes*] *parietina*, etc.)

produced zoospores. These in time developed into unicellular algæ, and by judicious management they produced several generations. Although they drew different ideas from this the Schwendenerians immediately took this as an argument for the dualism of lichens. Later (1872) Woronin confirmed the observations of Famentzin and Barentzky by his own experiments made with *Parmelia pulverulenta*.

When Schwendener propounded his theory one of the first to accept it was E. Bornet. He immediately began a series of observations and experiments to prove it. In his treatment of this subject (*An. de Sc. Nat.*, vol. 17, ser. 5) he divides his observations into two divisions corresponding to those of Schwendener—*i.e.*, those made upon lichens with chlorophyll-bearing gonidia, and lichens with phycochrome-bearing gonidia. Under the chlorophyll-bearing gonidia he found those belonging to such genera as *Trentepohlia*, *Phyllactidium*, *Protococcus*, *Cystococcus*, *Pleurococcus*, etc. He found the gonidia of several of the *Opegraphæ*, as *O. varia*, to be *Trentepohlia*. The branches of the alga were found ramifying the tissues of the bark, frequently going so far that the hyphæ of the lichen-fungus could not follow them. As they near the outer surface of the bark the hyphæ and algæ became more and more interlaced until they reached the thallus proper. When studied at all ages of the thallus the nature of the relations between the two were easily seen to be such as to preclude every chance of the one being developed from the other. The study of other lichens with similar gonidia, as *Verrucaria nitida*, *Rocella phycopsis*, *Chiodecton nigrocinctum*, etc., led to the same conclusions.

The gonidia of *Opeg. felicina* he found to be a *Phyllactidium*. The broad thallus of this alga was so large that the hyphæ did not entirely envelop it, but by gradually branching, surrounded parts of it and even sent small branches into it. He found in an old thallus of *Opegrapha varia* the normal filaments of *Trentepohlia* together with sporangia, showing that it could not be the "first stage of the lichens," but was an entirely separate plant. He sowed the spores of *Physcia* (*Theloschistes*) *parietina* on *Protococcus viridis*, and found that the hyphæ of the germinating spores readily enveloped the algæ, and did not envelop any other objects with which they came in contact. He also sowed spores apart from the algæ, and although germinating and producing hyphæ as did the others, they produced no gonidia and died as soon as the nourishment from the spore was consumed. He obtained similar results with *Biatora muscorum*.

As to those lichens containing phycochromogonidia, he found that *Colothrix* furnished gonidia for *Lichina pygmaea* and *confinis*; *Scytonema* and *Lyngbya* were found in such genera as *Pannaria*, *Erioderma*, and *Stereocaulon* (*Cephalodia*); *Nostoc* was found in *Collema* and allied genera; *Etigonema* in *Ephebe*, *Spilonema*, etc.; and *Glœocapsa* in *Synallisa*, *Cora*, *Omphalaria*, and similar genera. Sometimes he found the alga to be very little changed by the parasitism as in *Ephebe* and *Spilonema*; at others they were so changed as to be recognized only with difficulty. Two modes of contact were noticed: 1. Where the hyphæ are applied simply to the surface of the algæ, as in *Peltigera*, *Stictina*, etc. 2. Where the hyphal branches enter the algal cells, as in *Physcia*, *Omphalaria*, etc. From these observations he draws the following conclusions: that since *Trentepohlia*, *Phyllactidium*, etc., are so complex in their nature, and since no instance of the hyphæ enlarging and producing them has been found, and since these algæ (*Phyllactidium*, *Trentepohlia*, *Nostoc*, *Protococcus*, etc.) are found in the free state, there can be no doubt of the dual nature of those lichens containing them, and that, 1st, all gonidia can be referred to some algal type; and, 2d, the relations between hyphæ and gonidia are such as to exclude all possibility of one being produced from the other, and the theory of parasitism alone can explain these relations satisfactorily.

Reess made a series of cultivations with spores of *Collema glaucescens* sown with *Nostoc lichenoides*. By careful manipulation he produced a complete *Collema* thallus, but lacking the fruits. He saw the germinating spores "send out hyphæ which branched and forced themselves into the *Nostoc*."

Treub used the gonidia of one species of lichen and the spores of another. His success was similar to that of Reess.

Stahl uses the hymeneal gonidia and spores of *Endocarpon pusillum* and spores of *Thelidium minutulum*. He succeeded in producing a fully developed thallus, showing that these hymenial gonidia are ejected at the same time as the spores, to serve as gonidia for the young plants. He cultivated these hymenial gonidia separately, and found them to grow and divide just as do the undoubted unicellular algæ. Lately Bounier has succeeded in producing a complete lichen thallus with mature fruits by using lichen spores and algæ.

Among the botanists in the United States who have favored Schwendenerism in their later works are Dr. Asa Gray, Dr. Bessey, H. Willy, etc.

Most of the English lichenologists, together with Koerber, Nyland-

er, and Th. Fries, oppose the theory of "dualism of lichens." There are, however, several different ideas as to the origin of the gonidia, Fries holding one opinion, Nylander another, and Crombie, taking a mean between the two, seems to believe either. Muller supports the "micro-gonidia" theory of Dr. Minks, as did the lamented Professor Tuckerman. Nylander, while acknowledging the external similarities between lichens and ascomycetous fungi, asserts, as does Crombie, that there are too many differences between them to admit of their being placed together. "The hyphæ of lichens," he says, "are perennial, tough, thick-walled, straight, and insoluble in hydrate of potassium, while the hyphæ of all fungi are soft, thin-walled, flexuous, immediately dissolved in hydrate of potassium." Besides the "Lichenian reaction" is seen in all lichens and in none of the fungi. Both these points are denied by many eminent lichenologists and fungologists. De Bary has found the "Lichenian reaction" in several undoubted fungi. Hartog, de Seynes, etc., say that fungal hyphæ are no more soluble in hydrate of potassium than are lichen hyphæ.

Nylander also speaks of the "improbability" of the lichen hyphæ being endowed with the reason and sagacity necessary to search out a peculiar kind of algæ which it may imprison and press into service."¹ He further urges, as does Crombie and others, that no algæ will grow in such bare, exposed places as those chosen by most lichens. Cooke, who uses this same argument, says further that those lichens that do grow in low, wet places, as *Collema*, etc., are by some authors supposed to be algæ themselves and therefore should not be used in an argument for Schwendenerism. Nylander, however, takes an opposite view and places many of the algæ of Schwendener and Bonet, etc. (such as *Sirosiphon*, *Scytonema*, *Stigonema*, *Nostoc*, *Trentepohlia*, etc.) among the lichens, as he has found fruits upon them. But he finds no hyphæ. From these discoveries he argues that even if there is parasitism, it is not that of a fungus upon an alga, but rather of a lichen upon a lichen. He was one of the first to place *Cora* among the lichens.

Crombie says that finding and producing of zoospores in free gonidia does not prove that gonidia are identical with algæ, but that they are *only similar to them*.

The autonomists raise quite an objection as to the relative size of

¹ Why is it that any parasite, either vegetable or animal, is generally limited to but one or at most to but a few species upon which it feeds?—Heredity, etc.

"Parasite" and "Host," and insist that there can be no such a thing as a "mutual benefit" parasitism in nature as is claimed to be present in case of the lichen-fungi and the algæ. The latter objection Sargent explains (*Am. Mo. Mic. Jour.*, Feb., 1887) by saying that while the algæ furnish the necessary nourishment for the fungus, the latter in turn protects the former from excessive dryness and sunshine, allowing only enough softened light as is necessary to decompose the carbon dioxide, and, by acting as a sponge, takes up water readily and retains it, thus insuring at least a moderate supply of water for the algæ even in dry weather; moreover, it is a well-known fact that fungi in growing give off carbonic dioxide. This the lichen hyphæ furnish to the algæ, and they in turn give back oxygen, etc., to the hyphæ. As to the fact that some lichens grow in comparatively dry places, he thinks that this is not a very serious objection, since in some lichens we have hymenial gonidia which are ejected together with the spores; in others soredia, by means of which new plants can be formed without the aid of spores. Again, the species of algæ supposed to act as gonidia are those species that have become adapted to the frequent dry spells incident to terrestrial life. He further insists that the differences between the fungal-algal elements of a lichen and free-living fungi and algæ are just those differences that would result from the parasitical relationship claimed by the dualists.

Nylander says that in no case do the gonidia arise from the hyphæ, but from the parenchymatous cortical cells observed by him in the prothalline filaments of germinating spores. Crombie formerly held that the gonidia might come from the hyphæ or the hyphæ from the gonidia. Later, he says the gonidia are of thalline origin. He claims to have seen the germination of spores and growth of young lichen thalli on rocks, etc., where no algæ or gonidia could be seen. At first only the young hyphæ were seen. Later, gonidia were found. These he believes to have originated in certain glomerules noticed on the young hypothallus. These glomerules he claims contain gonidia in various stages of development. They finally become thicker and form the cortical layer. He then uses Nylander's explanation as to the free state of the gonidia in the interior of the thallus: "The cortical stratum gradually increasing and extending is at the same time dissolved (resorbed, physiologically speaking) beneath, and the gonidia consequently become free." Crombie says further that "the contact between the hyphæ and gonidia is in no way genetic or parasitic. . . . The gonidia are

neither adnate to or penetrated by the hyphæ, but only adherent to them by the lichenin. . . . In all cases the apparent union is simply amylaceous adherence, and the fancied penetration the result of erroneous observation." He says that Stahl's observations are of no account, as he is a very careless observer, etc.

Koerber, who is one of the best of observers, while he opposes Schwendener, admits that "the germinating spores must have free gonidia belonging to the same species in order to develop a complete thallus," but that "these gonidia are not algæ belonging to the lichens as a fungus, but *gonidia* previously separated from the thallus and which have become 'asynthetic.'" He practically admits the whole thing.

Hartog says, speaking of Crombie's arguments, that he either utterly ignores the strongest points in favor of "Parasitism" or laughs at them and says "improbable," or that they are the result of "poor work" and "erroneous observation." To use a favorite Cookian phrase, both Cooke and Crombie answer many of the best arguments in favor of "Dualism of Lichens" simply by "rhetoric."

It is a noticeable fact that in a new country where new groves of trees are being planted, before the trees show any signs of lichens they are covered, especially on the north side, by "green slime," and the thicker the "green slime" the more rapid is the growth of the lichens when they do appear. Again, it is noticeable that when lichens begin to grow on fences and trees they take the dampest, coolest, shadiest places first, and gradually, if it all, extend to the dryer places, as seen on fences where boards cross the posts, where the lichens may be seen to extend a short way from the post along the centre of the board, avoiding the dry, windy edges. Our largest lichens are almost always found in the darkest woods. These facts show that lichens in general are not the "lovers of light, dry places," as one author claims. But on the contrary, while they do not choose such places as do the saprophytic fungi, they generally choose places where plenty of the lower algæ are to be found.

Most of the botanists who have made any experiments with spores, gonidia, and algæ have obtained results conclusive enough to convince them that Schwendener is right.

In conclusion, we now have lichens belonging to the Ascomycetes, the Hymenomycetes, and the Gastromycetes, according to most of our latest and best authors. The gonidia are pretty conclusively proven to be algæ, notwithstanding Crombie's "rhetoric;" and the

parasitism of the fungus hyphæ on the algæ has not only been shown to be possible but quite probable, and to be the only way to explain the peculiar relations existing between hyphæ and algæ satisfactorily. Schwendenerism, like "The Heterocism of Rusts," may be considered as a settled fact, and our "beloved lichens" must sooner or later be placed among the fungi, where they rightly belong.

The University of Nebraska, Dec., 1888.

AMONG THE ANCIENT GLACIERS OF NORTH WALES.

BY F. JOHNSTON EVANS.

THERE are few spots in the British Isles which present so many attractions to the geological tourist as that most picturesque of localities into which the traveller by rail from Holyhead is suddenly ushered when the "Wild Irishman" express, which had been rushing at the rate of some sixty miles an hour across the Island of Anglesea, after emerging from the Menai tunnel, somewhat abruptly pulls up at Bangor station. Around on every side are piled strange rock formations, tilted and upturned in every conceivable fashion. Within a comparatively short distance are the famous slate quarries of Penrhyn, in themselves a beautiful study; while in nearly an opposite direction are visible the lofty summits of Snowdon and Cader-Idris. Let the reader accompany me in imagination into the midst of this magnificent mountain region, our special object being to wander and speculate, for a brief space, among the ancient glaciers of North Wales. Proceeding through the Vale of Llanberis, we perceive, lying high above the road, near the top of the pass, a huge block of stone which has long attracted the notice of even the least observant traveller. It is perched on the edge of a rock a few hundred feet above the bottom of the valley, on its northern flank—that is to say, on the left hand of the traveller who is ascending the pass. It is from fifteen to twenty feet long, and six or seven feet high, sharp and angular as on the first day that it was detached from the parent mass. It rests on a face of rock which, for a few feet, slopes sharply towards the valley beneath, and then ends in a perpendicular face of rock, and it is so lightly poised on its narrow base, that